Coastal Range and Movements of Common Bottlenose Dolphins off California and Baja California, Mexico

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Abstract.—Range and movement data from boat-based photo-identification surveys of Pacific coast common bottlenose dolphins (*Tursiops truncatus*), carried out over a 6-yr period from 1996 to 2001, were collated and analyzed. Primary data sources were from surveys carried out in four Southern California Bight study areas: Ensenada (12 surveys), San Diego (95 surveys), Santa Monica Bay (170 surveys) and Santa Barbara (61 surveys). Additional data from surveys in Monterey Bay between 1990 and 1993 (84 surveys) were also included in some analyses. Photographic matches between the San Diego, Santa Monica Bay and Santa Barbara study areas ranged from a low of 42% to a high of 67% and averaged 53%. In addition, 32 of the 58 individuals (55%) identified in Monterey Bay also occurred in one or more of the four Southern California Bight study areas. Back-and-forth inter-study area movements recorded between 1996 and 2001, were exhibited by 157 of the 246 (52%) individuals sighted in two or more study areas. Minimum travel distances ranged from 104 to 965 km, with one individual documented to have traveled from Ensenada to Monterey Bay. The most rapid travel speed was 94.5 km/day. These results reinforce earlier characterizations of coastal bottlenose dolphins being highly mobile and capable of rapid travel along the Baja California and the southern and central California Pacific coastline. It is hypothesized that these extensive movements are related to fluctuations in local, regional and perhaps Pacific-wide oceanic conditions that affect prey productivity and availability; combined with unique foraging strategies that have developed to meet these environmental fluctuations.

Bottlenose dolphins (*Tursiops truncatus*) occur as two distinct ecotypes along the California coast. The coastal form is typically found within 1 km of shore (Carretta et al.

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1998; Defran and Weller 1999; Ward 1999; Bearzi 2005) while the offshore form is distributed in deeper offshore waters, typically greater than a few kilometers from shore (Defran and Weller 1999; Bearzi et al. 2009; Carretta et al. 2013). These two ecotypes are managed by the National Marine Fisheries Service as separate population stocks (Carretta et al. 2013). Previous boat-based photo-identification surveys of coastal ecotype bottlenose dolphins within the Southern California Bight were carried out between 1981 and 1989 off San Diego, California (Hansen 1990; Defran and Weller 1999). Some surveys, using similar methodology, were also carried out in other areas off California and Baja California, Mexico, including Ensenada, Orange County and Santa Barbara (Fig. 1, Hanson and Defran 1993; Defran et al. 1999).

Abundance estimates for the coastal population, based on photo-identification surveys carried out in northern San Diego County from 1981 to 2005, estimated a population size (marked and unmarked dolphins combined) of about 450–500 (Dudzik et al. 2006; Carretta et al. 2013). Further, most individual dolphins were sighted four times or less and none appeared to be year-round or even seasonal residents of the San Diego area (Defran and Weller 1999). In contrast, some individuals in Santa Monica Bay were suggested to use that area on a seasonal basis (Bearzi et al. 2005). Additionally, a high proportion of the dolphins photo-identified in Ensenada (88%), Orange County (92%) and Santa Barbara (88%) were also sighted in San Diego (Defran et al. 1999). This inter-area overlap in sightings between widely separated study areas within the Southern California Bight explained the lack of site fidelity observed off San Diego. Further, "back and forth" travel between study areas was observed for many individual dolphins, suggesting that such inter-area movements were not a case of permanent emigration or immigration (Defran et al. 1999).

Bottlenose dolphins found in California's coastal waters differ in their range characteristics from other well-studied populations of the species (Wells et al. 1987; Weller 1998; Maze and Würsig 1999; Krützen et al. 2004; Waring et al. 2011). Some bottlenose dolphins along the US Atlantic Seaboard, Gulf of Mexico, and western Australia use semi-enclosed bays and estuaries and commonly demonstrate high levels of site fidelity, often persistent and year-round, to these protected habitats. The range characteristics of bottlenose dolphins found in the nearshore open coastal habitats of the Atlantic and Gulf of Mexico, as well as other locations, are not well understood. However, some seasonal movements occur along the Atlantic coast and the central west coast of Florida, but the geographic extent and temporal scale of such movements are not known (Waring et al. 2011).

Subsequent to the aforementioned 1981–1989 photo-identification research by Defran et al. (1999), studies on coastal bottlenose dolphins off California were initiated in Santa Monica Bay (1997–2001) and Monterey Bay (1990–1993)[1]; (Bearzi 2005). Supplementary studies extending the time-series of data for San Diego (1996–1999) were also conducted (Dudzik 1999; Lang 2002). Additional surveys were completed in Ensenada (1999–2000)[2] and Santa Barbara (1998–1999), where previous effort was low and the number of individuals identified relatively limited (Lang 2002) (Table 1). In combination, these new data allowed for the more comprehensive and contemporary

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[1] Feinholz, D.M. 1996. Pacific coast bottlenose dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.Sc., San Jose State University, Moss Landing Marine Laboratories, Moss Landing, CA.

[2] Guzòn-Zatarain, O.R. 2002. Distribuciòn y Movimientos del tursiòn, *Tursiops truncatus (Montagu, 1821)* en la Bahìa de Todos Santos, Baja California, Mèxico (Cetacea: Delphinidae). Master thesis, Facultad de Ciencias Marinas, Universidad Autonoma de Baja California, Ensenada, Mèxico.

Fig. 1. Map of California and Baja California, Mexico coastal study area locations: Ensenada, San Diego, Santa Monica Bay, Santa Barbara and Monterey Bay. Point Conception and Punta Colonet are the northern and southern coastal boundaries of the Southern California Bight.

Table 1. Summary information on survey effort, study period, photographic data, and data sources for all study areas.

Study area	Number of surveys (complete, partial)	Study period	Number of dolphins identified
Ensenada[1]	12 (12, 0)	1999–2000	81
San Diego[2]	95 (48, 47)	1996–1999	292
Santa Monica Bay[3]	170 (44, 126)	1997–2001	245
Santa Barbara[4]	61 (43, 18)	1998–1999	182
Monterey Bay[5]	84 (16, 68)	1990–1993	58

Data sources: [1] Guzòn-Zatarain, O.R. (2002). Distribuciòn y Movimientos del tursiòn, *Tursiops truncatus (Montagu, 1821)* en la Bahìa de Todos Santos, Baja California, Mèxico (Cetacea: Delphinidae). Master thesis, Facultad de Ciencias Marinas, Universidad Autonoma de Baja California, Ensenada, Mèxico; [2] Dudzik (1999), [2,4] Lang (2002); [3] Bearzi (2005); [5] Feinholz, D.M. (1996). Pacific coast bottlenose dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.Sc., San Jose State University, Moss Landing Marine Laboratories, Moss Landing, CA. Some numbers differ from those given in these data sources due to refinement and revision of the dataset over time and the elimination of sightings not meeting the specified photographic quality criteria.

assessment of spatial and temporal range characteristics of California coastal bottlenose dolphins presented here.

Materials and Methods

The general design of the present study was the same as that used by Defran et al. (1999) and is similar to others studies that have carried out photo-identification catalog comparisons between independently collected data sets for a particular species (e.g., Weller et al. 2012).

Study Areas

Five distinct geographic regions along the California (San Diego, Santa Monica Bay, Santa Barbara, Monterey Bay) and Baja California, Mexico (Ensenada) coastline served as study areas (Figs. 1 & 2). While all of these study areas were generally similar, they differed from one another in the geographic extent of the coastline surveyed and in some characteristics of the nearshore topography and bathymetry (Dailey et al. 1993; Defran and Weller 1999; Defran et al. 1999; Bearzi 2005). Coastal areas surveyed were non-contiguous and ranged from Ensenada, Baja California (31°42′N, 116°40′W) in the south to Monterey Bay, California (36°58′N, 121°55′W) in the north, covering a total distance of 980 km. The locations and lengths along the coastal contour of the five study areas and the distances between their boundaries are given in Fig. 2.

Photo-Identification Surveys and Photographic Data Analysis

Similar survey methodology and photo-identification procedures were used in all study areas. Detailed descriptions of these procedures are provided elsewhere (Defran and Weller 1999; Dudzik 1999; Lang 2002; Bearzi 2005) but are briefly described here. Photographic surveys involved slow travel in small boats while moving parallel to the coast and outside the surf line; generally within 250–500 m of shore and corresponding to water depths between 4 m to 10 m (Ward 1999). Surveys were conducted in sea state and visibility conditions adequate for finding and photographing dolphins. Although past data clearly demonstrate that most coastal bottlenose dolphins are found within 500 m of
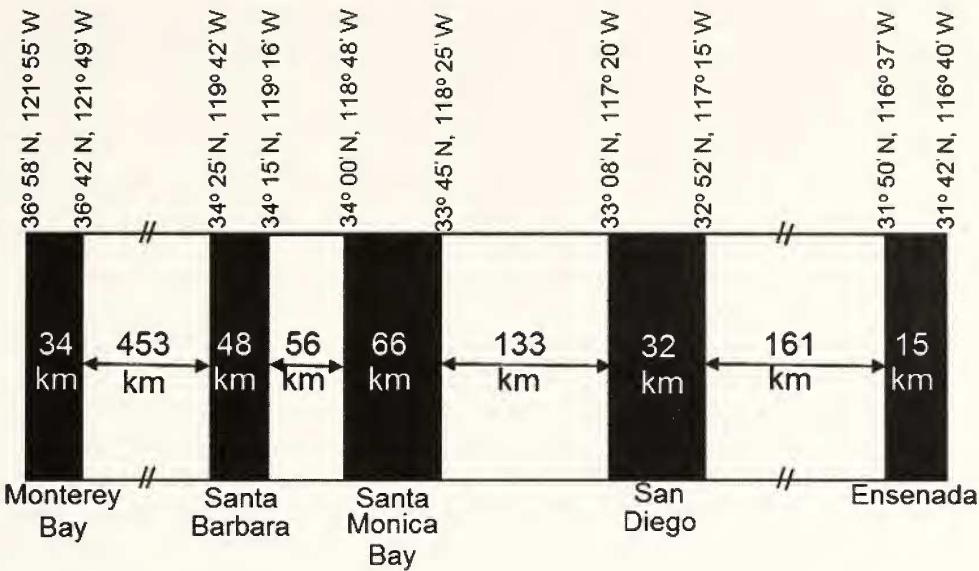
Fig. 2. Study area dimensions, coordinates and distances between study areas.

the shore (Hanson and Defran 1993; Carretta et al. 2013), two or more observers nevertheless visually searched the area from the shore to ~ 2 km offshore to ensure complete coverage of the nearshore survey strip. Once a group of dolphins was sighted, initial estimates of group size, as well as information on time, location, environmental conditions and behavior were recorded.

Following initial estimates of group size, the vessel maneuvered to a distance from the dolphins suitable for photo-identification. Using high-speed SLR cameras equipped with telephoto lenses, attempts were made to photograph every dolphin (marked and unmarked) within a group. Initial estimates of group size were revised as necessary, and contact with the group was maintained until photographic effort was completed. Identical procedures were repeated as the vessel resumed travel on the predetermined survey route and as additional dolphin groups were encountered.

In Monterey Bay and Santa Monica Bay, surveys did not always cover the entire study area. The Monterey Bay study area was divided into two sectors of approximately equal length[3]. Sixteen out of 84 surveys were complete and covered both sectors, while 68 were partial, covering only one sector (Table 1). In Santa Monica Bay, the study area was too large to be surveyed in one day. Thus, on a given day, surveys generally covered only the "northern" or "southern" portion of the entire study area (Bearzi 2005). When both the northern and southern portions of the study area were surveyed within several days, a complete survey was scored. Otherwise, surveys of all or only a part of the southern or northern portion of the study area were scored as partial surveys (Table 1).

Only clear photographs of dorsal fins with two or more distinctive dorsal fin notches were used for analysis. Distinctive dorsal fins were those that had sufficient notching on the trailing or leading edge such that they could be matched to high quality dorsal fin photographs from other sightings (Urian and Wells 1996; Defran and Weller 1999;

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[3] Feinholz, D.M. 1996. Pacific coast bottlenose dolphins (*Tursiops truncatus gilli*) in Monterey Bay, California. M.Sc., San Jose State University, Moss Landing Marine Laboratories, Moss Landing, CA.

Table 2. The percent of inter-study area occurrence for individuals seen in San Diego, Santa Monica Bay, and Santa Barbara (left column) with individuals seen in the Ensenada, San Diego, Santa Monica Bay and Santa Barbara comparison study areas between 1996-2001. For example: 35 of the 81 (43%) dolphins seen in Ensenada were also seen in San Diego ($n = 292$).

	Number of individuals (1996–2001)	Ensenada	San Diego	Santa Monica Bay	Santa Barbara
San Diego	292	43% (35/81)	-	58% (142/245)	67% (122/182)
Santa Monica Bay	245	22% (18/81)	49% (142/292)	-	57% (104/182)
Santa Barbara	182	9% (7/81)	42% (122/292)	42% (104/245)	-

Defran et al. 1999; Mazzoil et al. 2004). Only unambiguous matches were accepted as resightings.

Dorsal fin photographs from all study areas except Santa Monica Bay were analyzed and maintained in the Cetacean Behavior Laboratory (CBL) at San Diego State University. The photographic catalogs from Ensenada, San Diego, and Santa Barbara consisted of 397 individuals identified between 1996 and 2000, while the photographic catalog from Monterey Bay consisted of 58 individuals identified between 1990 and 1993. The Santa Monica Bay photographic catalog consisted of 245 individuals identified from 1997 to 2001. Finally, the one or two best images of each individual from the CBL and Santa Monica Bay catalogs, originally acquired in film format, were digitally scanned, and sighting histories from all six study areas were integrated into one comprehensive database.

Dorsal fin images collected in Santa Monica Bay were cross-matched to all images in the CBL catalog using techniques described in Mazzoil et al. (2004), with a few modifications. The matching process began by reviewing and verifying all previously judged matches in both catalogs. Each individual was initially assigned to category 1, 2, 3 or 4 depending on the location of the most distinctive dorsal fin notch. Then, Santa Monica Bay images were compared to all CBL images in that same category. If no match was found, the image was compared to the CBL images in all remaining categories. If a match was found, the Santa Monica Bay individual was assigned a "project number" to match the CBL individual. If no match was made between the Santa Monica Bay and CBL images, a new individual was added to the project catalog as a new "type specimen."

Results

The primary data sources used for analysis were from surveys carried out between 1990 and 2001 in four Southern California Bight study areas: Ensenada (12 surveys), San Diego (95 surveys), Santa Monica Bay (170 surveys) and Santa Barbara (61 surveys). Additional data from surveys conducted in Monterey Bay between 1990 and 1993 (84 surveys) were included in some analyses as noted below.

Inter-Study Area Occurrence

The primary analysis of inter-study area occurrence consisted of comparisons involving the entire dataset of individual sightings ($n = 470$) acquired within the Southern California Bight study areas of Ensenada, San Diego, Santa Monica Bay and Santa Barbara between 1996–2001. An additional analysis involved a comparison of 58 dolphins identified in Monterey Bay between 1990–1993 to the 470 identified in the Southern California Bight from 1996–2001. In all cases, comparisons between study areas involved the percent of all individuals from one study area that were also sighted in another study area. For example, 35 of the 81 (43%) dolphins seen in Ensenada were also seen in San Diego (Table 2).

Thirty-two of the 58 individuals (55%) identified in Monterey Bay also occurred in one or more of the four Southern California Bight study areas between 1996 and 2001. Inter-study area occurrence of individual dolphins in the 1996–2001 Southern California Bight dataset was highest between San Diego and Santa Barbara (67%), followed by decreasing overlap between San Diego and Santa Monica Bay (58%), Ensenada and Santa Monica (22%) and finally Ensenada and Santa Barbara (9%) (Table 2).

Inter-Study Area Back-and-Forth Movements

Among the 470 dolphins identified in the combined 1996–2001 Southern California Bight catalog, 246 (52%) were sighted in two or more study areas. Of these, 157 individuals (64%) exhibited 'back-and-forth' movements between study areas (see also Defran et al. 1999). Back-and-forth movements were scored when a dolphin was seen in one study area (e.g., San Diego), subsequently resighted in another study area (e.g., Santa Monica Bay), and then, having apparently reversed direction, was later resighted in a study area in the opposite direction (e.g., San Diego or Ensenada). Among the 157 dolphins that exhibited back-and-forth movements, 85 individuals (54%) exhibited such 2–6 times.

Dolphins exhibiting the most frequent back-and-forth movements in the shortest amount of time included two individuals: dolphin no. 3383 made five movement reversals within 18 months (Fig. 3A) and dolphin no. 2108 made four movement reversals within seven months (19 March 1998 to 5 October 1998). Dolphin no. 4422 (Fig. 3B) made six movement reversals, the maximum number documented, during a four-year period. Finally, dolphins exhibiting back-and-forth movements were most frequently observed in the San Diego, Santa Monica Bay, and Santa Barbara study areas, where the most surveys were conducted. Conversely, the fewest dolphins exhibiting back-and-forth movements were observed in Ensenada and Monterey Bay, where the fewest surveys were conducted.

Travel Distance and Travel Speed

For the 246 dolphins sighted in at least two study areas, the distances between their two most widely separated sighting locations were calculated (Fig. 4). The majority of these 246 dolphins (85%, $n = 209$) were documented to travel between 104 and 400 km. At the minimum, one dolphin (no. 2780) was documented to travel only 104 km from Santa Monica Bay to Santa Barbara. At the maximum, one dolphin (no. 3426) was observed in both Ensenada and Monterey Bay, a travel distance of 965 km.

Many of the surveys conducted between 1996 and 2001 in the Ensenada, San Diego, Santa Monica Bay and Santa Barbara study areas were carried out relatively close in time, which allowed for the calculation of minimum travel speeds between different locations. Three noteworthy case studies demonstrating particularly rapid travel included: (1) dolphin no. 4643 traveled 318 km from San Diego to Santa Barbara in six days (18 June to 24 June 1999), resulting in a minimum travel speed of 53 km/day; (2) dolphin no. 2221 traveled 300 km, also from San Diego to Santa Barbara, in five days (28 February to 5 March 1999), resulting in a minimum travel speed of 60 km/day; and (3) dolphin no. 3656 traveled 177 km from Santa Monica Bay to San Diego in a 12 day period (2 November to 14 November 1998), and then was sighted two days later (16 November 1998) 189 km back in Santa Monica Bay. The movement between San Diego and Santa Monica Bay in two days represents the fastest travel speed (95 km/day) recorded during the study.
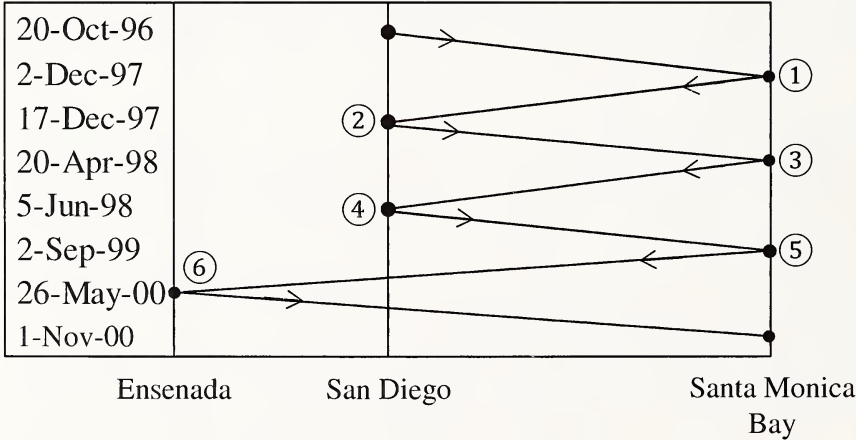
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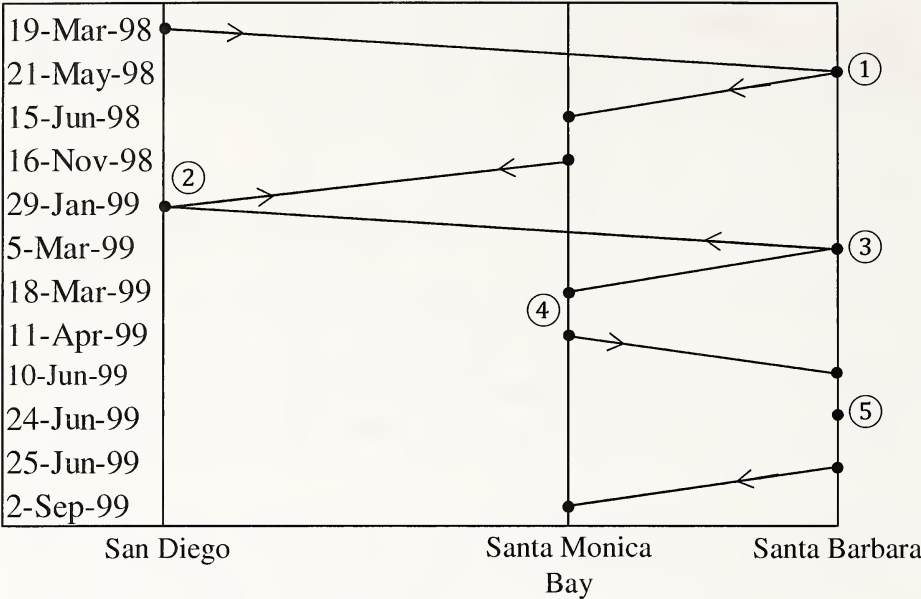
3B

Fig. 3A. Dolphin no. 3383 exhibited five inter-study area movements between 19 March 1998 and 2 September 1999. Circled numbers indicate a direction of movement reversal and arrows represent the direction of travel. Fig 3B. Dolphin no. 4422 exhibited six reversals between 20 October 1996 and 1 November 2000.

Discussion

Range and Movement Comparisons

The movements of coastal bottlenose dolphins reported herein were generally similar to results from an earlier study on the range and movement characteristics of this population between 1981–1989 (Defran et al. 1999). In that study, dolphins showed a
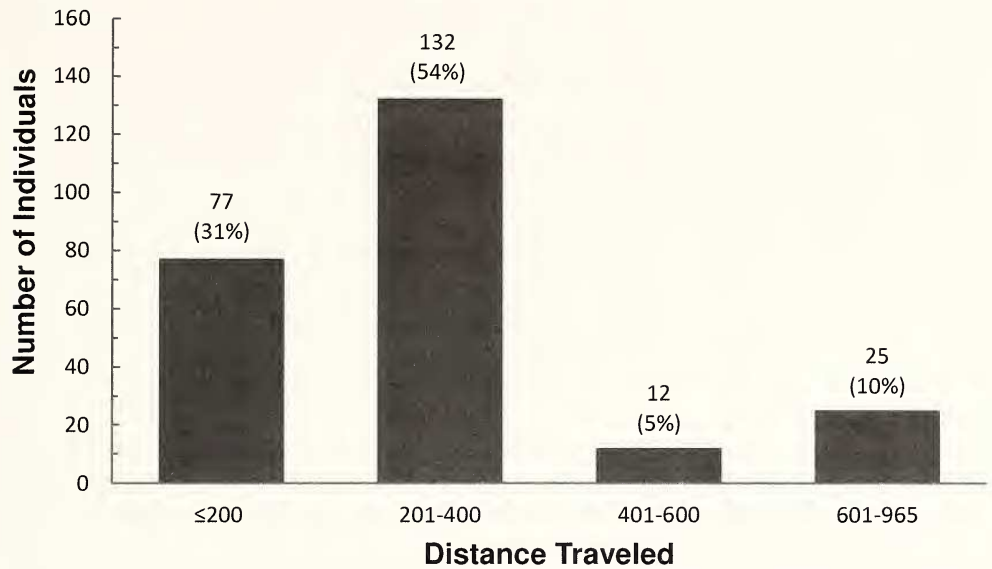
Fig. 4.   Minimum estimates of distances traveled for 246 identified dolphins that were sighted two or more times between 1996 and 2001.

high degree of travel between San Diego and other study areas in the Southern California Bight, displayed regular inter-study area back-and-forth movements, and exhibited relatively rapid travel over extensive coastal distances. The most notable difference between the current results and those reported by Defran et al. (1999) was the somewhat lower percent of resighting overlap between the Southern California Bight study areas. For example, Defran et al. (1999) reported that between 88% and 92% of the dolphins identified in Santa Barbara, Ensenada and Orange County were resighted in San Diego (1981–1989 dataset). In the current study, inter-study area overlap between San Diego, Santa Monica and Santa Barbara ranged from 42% to 67% during the 1996–2001 study period. Overlap between Ensenada and the other study areas in the Southern California Bight between 1996 and 2001 was even lower, ranging from 9% to 43% (Table 2).

The causal mechanisms driving the lower levels of overlap between the Southern California Bight study areas is unresolved, but available information provides some support for the concept of coastal dolphins progressively expanding use of more northern portions of their range. Prior to the powerful 1982–83 El Niño, the presumed northern range limit for these dolphins was Pt. Conception. Subsequent to the 1982–83 El Niño, there were an increasing number of coastal dolphin sightings documented along the coastline from Pt. Conception to Monterey Bay (Table 1 in Wells et al. 1990). One of the earliest of these sightings was off the coast of Santa Cruz, CA. Photo-identification images from that sighting showed that nine of these dolphins had previously been identified off San Diego between 1981–1983 (Hansen 1990). Continued photo-identification studies carried out on dolphins in Monterey Bay between 1990–1993 confirmed that 55% of the dolphins identified there had previously been identified between 1981–1989 within the Southern California Bight (Hansen 1990; Defran and Weller 1999; Defran et al. 1999; this report). The nearly continuous presence of bottlenose dolphins in the Monterey Bay area from 1990 to the present indicates that the range extension described by Wells et al. (1990) has persisted (e.g., Riggin and

Maldini 2010; Maldini et al. 2010), and in fact, has further expanded into San Francisco Bay[4].

While these hypothesized changes in the northern distribution of the species seem plausible, it is less likely that similar changes were occurring to the south (e.g., Ensenada study area). That is, a shift (increase) in habitat use to the south would seemingly have resulted in higher inter-area resightings for Ensenada than those reported here (Table 2). Further support for an increased presence of coastal bottlenose dolphins in the northern portion of their range comes from the number of dolphins identified there. Over 300 coastal dolphins were photographically identified in Monterey Bay from 1990 to 2010 (Maldini et al. 2010) and 67 off Santa Barbara between 2009 and 2010. Interestingly, of the 67 dolphins identified off Santa Barbara, 31 (46%) have also been sighted in Monterey Bay[5], demonstrating a considerable amount of interchange between these two northern study areas.

It is also possible that increased research effort has contributed to more precise estimates of inter-study area occurrence. That is, survey effort, as well as the number of dolphins identified, especially in Ensenada and Santa Barbara, was considerably higher for the 1996–2001 dataset than it was for the 1981–1989 dataset. Further, the survey distance covered during Santa Monica Bay surveys (conducted only during 1997–2001) was considerably greater than that covered in other study areas. Taken together, the sample values used for assessing inter-area overlap during 1996–2001 may reflect the influence of greater effort, and thus may be more precise than the 1981–1989 dataset. The impact of regional and global oceanic events and trends such as El Niño, which occurred during and in close proximity to both the 1981–1989 and 1996–2001 sample periods, may have also played a role in the greater inter-area overlap observed in the 1981–1989 dataset. While this speculation about differences between the two datasets may be plausible, an alternative explanation is that lower inter-area overlap in the 1996–2001 dataset (compared to the 1981–1989 dataset) reflects a change in range characteristics for some individuals.

The range and movement patterns described herein, including those from Defran et al. (1999), are probably quite conservative estimates of these processes. By way of illustration, surveys within the six study areas (i.e., Ensenada, San Diego, Orange County, Santa Monica Bay, Santa Barbara and Monterey Bay) cover only 262 km of the 980 km coastline (extending from Ensenada to Monterey Bay). Further, even for the most contemporary research effort (1996–2001), surveys were carried out on only a very small percent of the 1,460 possible days in any study area. Therefore, our descriptions of the frequency and geographic scope of coastal bottlenose dolphin movement patterns are a byproduct of sampling effort.

Range and Movements Interpretation

Most interpretations of the spatial and temporal range characteristics of California coastal bottlenose dolphins have emphasized the primary role played by the nearshore distribution and abundance of dolphin prey (Weller 1991; Defran et al. 1999; Dudzik

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1999; Ward 1999; Lang 2002; Bearzi 2005). Dynamic variations in oceanic processes such as El Niño and La Niña, regional processes such as upwelling and variable expressions of the California Current System, and local substrate and habitat effects, are all presumed to play a critical role in prey availability.

The most integrated interpretation of the extensive coastal movements demonstrated by these dolphins stresses the interplay between environmental variables, prey item preferences and distributional characteristics, as well as behavioral repertoires and distinctive foraging strategies (Defran et al. 1999). While preferred prey items for Pacific coast bottlenose dolphins, such as surfperch (Embiotoridae) and croakers (Sciaenidae) are widely distributed along the eastern Pacific coastline, their abundance and distribution is unpredictable and patchy. An apparent and recurrent foraging response to this unpredictable distribution of prey is a pattern of movement within the nearshore zone referred to as "localized" and "directional" movement (Ogle 2005). During localized movement, dolphins move back-and-forth along shore in a restricted area, often of several kilometers or less. During directional movement, dolphins travel in the same direction, north or south, and parallel to the coast. When these movement types were compared, significantly more feeding occurred during localized movement and significantly more travel occurred during directional movement. In this case, localized movement was hypothesized to be foraging behavior related to a prey patch.

In light of the extensive longshore movements reported herein, we suggest that coastal bottlenose dolphins off California and Mexico are moving great distances in search of preferred but unpredictable nearshore prey patches. Once a prey patch is located, longshore directional travel (movement between patches) ceases and localized movement (movement within patches) commences. As local prey patches become depleted or are effectively 'fished,' dolphins "relocate" in search of more optimal conditions (Defran et al. 1999). This relocation strategy manifests itself in the type of inter-study area movements found during the current study.

Conclusions

The results presented here reinforce and extend earlier characterizations of coastal bottlenose dolphins being highly mobile along the central and southern California and Baja California coastline. More specifically, dolphins in this population routinely move distances of several hundred kilometers or more along the coastline. These extensive movements are thought to vary with fluctuations in local, regional, and perhaps Pacific-wide oceanic conditions which affect prey productivity and availability. In the extreme, dolphin groups alternate between back-and-forth movements over small stretches of coastline (several kilometers) while foraging on concentrations of preferred prey. When these prey concentrations are diminished, dolphins travel parallel to the coast, north or south, until they encounter another prey patch. Although many of the dolphins identified in this study were observed to use extensive coastal ranges, it is uncertain if some individuals use more limited core ranges. The small size of the coastal bottlenose dolphin population (<500) in combination with its affinity for very nearshore waters make them vulnerable to a number of human related threats including fishery-related mortality, pollution from coastal runoff and habitat degradation resulting from urbanization. Knowing that a substantial portion of this population moves along a nearly 1000 km long stretch of the coastline, including trans-boundary movements into Mexico, is of particular value to management objectives, particularly with respect to understanding potential risks to their survival.

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